DEVELOPMENT OF THE GEOGLOSSACEAE[1]

G. H. DUFF

Although a number of investigators have contributed developmental studies on the Ascomycetes and very substantial progress has been made, our knowledge of the ontogeny of the higher forms of these fungi is still far from complete. In consequence, our present systems of classification are full of gaps, and our conceptions of the affinities of these plants are often contradictory or mere guesses. For the elaboration of a satisfactory system of classification and for the consolidation of our ideas regarding relationships, it is requisite that the ontogeny of a much larger number of representative species be worked out.

This investigation has been confined to the Geoglossaceae. Observations have been made on practically complete stages of *Cudonia lutea*, *Spathularia velutipes*, and *Trichoglossum hirsutum*, and on some of the critical features of *Leotia*. Heretofore studies in this family have been restricted to three species of the genera *Leotia* and *Mitrula*.[2] The chief interest centers around *Cudonia lutea* and *Spathularia velutipes* because of the remarkable ascogonia possessed by these plants, and because of the conspicuous veils which render obvious to the naked eye their angiocarpous nature, and which have long stood in opposition to the distinction by which SCHROETER[3] separates the Helvellineae from the Pezizineae.

The youngest stage of *Cudonia lutea* which has come under observation is in the form of a minute cushion of interwoven threads measuring but 84 μ in height. At the center of this loose assemblage of threads may be seen a small but definite group of hyphae which are rendered conspicuous by their size and staining qualities. These are not ascogonia, as might at first be

[1] Preliminary communication.

[2] DITTRICH, G., Zur Entwickelungsgeschichte der Helvellineen. Cohn's Beiträge 8:1. 1918.

BROWN, W. H., The developement of the ascocarp of *Leotia*. BOT. GAZ. 50:443–459. 1910.

[3] SCHROETER, J., In ENGLER and PRANTL, Die natürlichen Pflanzenfamilien.

supposed, but are the precursors of coiling procarps which arise from them at a later stage, in a manner to be described.

So far as the writer is aware, such a sequence of structures has not elsewhere been reported for any species of the Ascomycetes proper. Among the lichens, however, a similar condition has been recorded. In a paper dealing with the ontogeny of the ascocarp of several forms of lichens, NIENBURG[4] figures and describes bodies which are differentiated early in the process of development, and which at a later stage give rise to "carpogones." These bodies are designated "generativen hyphen" by this author. Following his usage, the term "generative hyphae" will be employed in reference to the threads here described and to their immediate proliferations.

The next developmental stage exhibits a distinct differentiation of vegetative tissues. There is now present a well organized outer covering, which completely envelops the looser tissues, and at the center the generative hyphae are more conspicuous than ever. By this time the generative hyphae have proliferated to a slight extent, and appear as a somewhat larger and more compact group of threads with an extraordinary affinity for stains. As growth proceeds the outer tissue expands, remaining in its peripheral position as a true veil. Its persistence and growth are not functions solely of the tissues that lie beneath it, but of itself as well. By its own growth it is able to keep pace for a considerable time with the rapid enlargement of the cap, a fact that is true even of that portion which is eventually separated from its connections by the developing hymenium. This growth, in contrast with mere stretching, results in a marked increase in the thickness of the veil, measurements showing that the earliest envelopes average about 20 μ, while at maturity they approach 70 μ in thickness. The veil ruptures over the hymenium only, and there only after the latter is well matured.

By upward growth and by the appearance of a mass of what may be termed parenchymatous tissue at the base of the young fruit, the generative hyphae are forced to assume a subapical

[4] NIENBURG, W., Beiträge zur Entwickelungsgeschichte einiger Flechtenapothecien. *Flora* **98**: 1907–1908.

position. This position is retained until they give rise to the procarps. At this time the height of the fruit body is about 2 mm., and the cap has been well differentiated from the stem. At such a stage the generative hyphae largely fill the upper portions of the cap, and the procarps arise as branches from these hyphae. The procarps are numerous, coiling, and deeply staining structures, scattered irregularly throughout the cap. These coils are continued upward by what appear to be "typical" multiseptate trichogynes, which penetrate the envelope, projecting into the air for a short distance. Spermogonia and spermatia are entirely lacking, and it is not thought that the trichogynes are functional organs.

Despite the great difficulty of staining differentially both the generative hyphae and the procarps, owing to the remarkable affinity for stains exhibited by these structures, there is sufficient evidence to show that the cells of the procarp, including those of the trichogyne, are originally uninucleate. Later the ascogonial cells become multinucleate, the nuclei being small and paired; and ascogenous hyphae arise from them into which these nuclei probably pass.

It is important to note that up to this time there has been no sign of a hymenium. The fruiting surface now makes its first appearance in the form of paraphyses immediately beneath the veil. Before the paraphyses have attained their full development the ascogenous hyphae, that meanwhile have taken their origin from the procarps in close proximity, and have rapidly proliferated and gone through various evolutions of hook formation, begin to organize asci. This young hymenium is inclosed by the veil, and remains so until many of the asci are mature and spore discharge is ready to commence. The nuclear phenomena preceding spore formation are typical in their chief features.

The developmental history of *Spathularia velutipes* follows a course not unlike that of *Cudonia lutea*. The youngest fruits of this species that have been examined are somewhat larger than the youngest species of *Cudonia*, being in the neighborhood of 0.5 mm. in height. At this stage the young *Spathularia* is covered with an envelope, but the inner tissues are quite undifferentiated, and there are as yet no signs of any structures resembling the generative

hyphae of *Cudonia*. In the next stage of the series, however, threads resembling generative hyphae are visible, and they have already taken up their position just behind the apex of the somewhat cone-shaped ascocarp. The envelope here is worthy of some remark, inasmuch as it is easily differentiable by staining into two parts, an outer and an inner. The inner tissue is capable of growth and is responsible for the persistence of the veil in *Spathularia*, and for the continued production of the outer tissue which becomes split by the growth of the fruit body into adhering masses of cells which are responsible for the velvety appearance from which the species derives its name. Measurements of the thickness of the envelope in the youngest and in mature specimens here also indicate the extent of this growth, and show the veil to be capable of doubling in thickness, increasing from about 25 to 50 μ. This is but a rough and inadequate index, however, since the outer tissue may be considerably worn away.

Procarps of a very much reduced nature are produced in *Spathularia velutipes*. These appear even later than those of *Cudonia*, arising after the formation of paraphyses. They are more variable in size and shape, and do not possess trichogynes. They are responsible for the initiation of the paired condition of the nuclei, and ascogenous hyphae may be seen arising from them. The entire ascogonial system in *Spathularia* is just as refractory with respect to stains as that of *Cudonia*, and nuclear details, consequently, are very difficult to obtain. In all other respects *Cudonia* and *Spathularia* resemble one another closely.

Examination of a complete series from a very young stage to maturity has shown that *Trichoglossum hirsutum* is not possessed of a veil at any time in the history of the development of its fruit body. The long setae that characterize the ascocarp of this species, however, are present from the very first. This condition is noteworthy, inasmuch as it is very similar to that which FITZPATRICK[5] has described for *Rhizina undulata*. In these two species we have the only members of the Helvellineae whose developmental history has as yet been described, for which the presence

[5] FITZPATRICK, H. M., The development of the ascocarp of *Rhizina undulata* Fr. BOT. GAZ. **63**:282–296. 1917.

of a veil at some stage of their development has not been claimed, and each is provided with these remarkable setae. In matters of sexuality *Trichoglossum* appears to be still more reduced than *Spathularia*. Ascogenous hyphae arise from threads which are little if at all differentiated from the vegetative hyphae.

Although DITTRICH (*loc. cit.*) claims for *Leotia lubrica* the possession of a veil in its younger stages, BROWN (*loc. cit.*), in his more recent paper on this species, makes no mention of the occurrence of any such structure, and apparently has observed none. A tissue overlying the hymenium has been observed by the writer in a fairly well advanced specimen during the course of a cursory examination of this form. Younger stages which show this covering have not been found, however, so that considerable uncertainty obtains with regard to the identity of this tissue with that figured by DITTRICH.

A point of very great interest in this investigation is the close resemblance of the conditions described for these Geoglossaceae to those which NIENBURG attributes to the *Cladonia*-like lichens *Icmadophila*, *Sphyridium*, and *Baeomyces*. The occurrence in these lichens of generative hyphae which later give rise to carpogonia has already been mentioned. These carpogonia are "typical" coils with trichogynes in *Icmadophila;* but they are progressively more degenerate in *Sphyridium* and *Baeomyces*, in the last of which NIENBURG was unable to distinguish their presence with certainty. Further points of similarity include the occurrence of an envelope in the early stages, and the methods of ascus formation. This remarkable parallelism evidently represents a relationship. Although a general relationship between the Ascolichens and other ascomycete groups, such as the Discomycetes and Pyrenomycetes, has long been recognized, and although some lichenologists have advocated and attempted the distribution of the lichen genera among those of other Ascomycetes, a fundamental basis of relationship between the discolichens and the order Helvellineae has been wanting. This basis is supplied here and consists of a close similarity in developmental history, particularly with regard to the veil and to the manner and time of appearance, number, position, and condition of procarps. As our knowledge of these

forms increases, the extent of this relationship will unquestionably be more clearly shown.

A detailed illustrated account of this work is to be published in the near future.

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UNIVERSITY OF TORONTO
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